Growth responses of subalpine fir to climatic variability in the Pacific Northwest

David W. Peterson, David L. Peterson, and Gregory J. Ettl

Abstract: We studied regional variation in growth-limiting factors and responses to climatic variability in subalpine forests by analyzing growth patterns for 28 tree-ring growth chronologies from subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) stands in the Cascade and Olympic Mountains (Washington and Oregon, U.S.A.). Factor analysis identified four distinct time series of common growth patterns; the dominant growth pattern at any site varied with annual precipitation and temperature (elevation). Throughout much of the region, growth is negatively correlated with winter precipitation and spring snowpack depth, indicating that growth is limited primarily by short growing seasons. On the driest and warmest sites, growth is negatively correlated with previous summer temperature, suggesting that low summer soil moisture limits growth. Growth patterns in two regions were sensitive to climatic variability associated with the Pacific Decadal Oscillation, apparently responding to low-frequency variation in spring snowpack and summer soil moisture (one negatively, one positively). This regional-scale analysis shows that subalpine fir growth in the Cascades and Olympics is limited by different climatic factors in different subregional climates. Climate–growth relationships are similar to those for a co-occurring species, mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière), suggesting broad biogeographic patterns of response to climatic variability and change by subalpine forest ecosystems in the Pacific Northwest.

Résumé : Les auteurs ont étudié la variation régionale des facteurs qui limitent la croissance et les réponses à la variabilité climatique de forêts subalpines en analysant les patrons de croissance de 28 séries dendrochronologiques établies à partir de peuplements de sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.) situés dans les Cascades et les monts Olympic (Washington et Oregon, États-Unis). Une analyse factorielle a identifié quatre séries temporelles distinctes de patrons de croissance communs; le patron de croissance dominant dans tous les sites varie en fonction de la précipitation annuelle et de la température (altitude). Dans la plus grande partie de la région, la croissance est négativement corrélée à la précipitation hivernale et à la hauteur de neige accumulée au printemps, ce qui indique que la croissance est surtout limitée par de courtes saisons de croissance. Dans les sites les plus chauds et les plus secs, la croissance est négativement corrélée à la température de l'été précédent, indiquant qu'une faible quantité d'humidité dans le sol en été limite la croissance. Les patrons de croissance de deux régions sont sensibles aux variations climatiques associées à l'Oscillation Décennale du Pacifique, en répondant apparemment à la variation de basse fréquence de la couverture nivale au printemps et de l'humidité du sol en été (négativement dans un cas et positivement dans l'autre). Cette analyse à l'échelle régionale montre que la croissance du sapin subalpin dans les Cascades et les monts Olympic est limitée par des facteurs climatiques différents dans des climats sous-régionaux différents. Les relations entre la croissance et le climat sont similaires à celles d'une espèce cooccurrente, la pruche des montagnes (*Tsuga mertensiana* (Bong.) Carrière), ce qui suggère l'existence de larges patrons biogéographiques de réponse à la variabilité et au changement climatique dans les écosystèmes forestiers subalpins du Nord-Ouest du Pacifique.

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Introduction

Forest responses to future climatic variability and change are difficult to predict with confidence because of a lack of information about climatic influences on tree growth, survival, and species distributions. Although forest succession ("gap") models simulate changes in forest species composition in response to climatic variability and change (Davis and Botkin 1985; Solomon 1986; Urban et al. 1993), more realistic parameterization with regard to species growth responses to climatic variability is needed to make accurate predictions. Biogeographic models predict shifts in species ranges in response to climatic changes, based on the assumption that species will migrate to maintain their current distributions with respect to climate-related environmental

variables (Sykes et al. 1996; Lenihan and Neilson 1995; Bartlein et al. 1997); however, the environmental factors controlling species distributions are often unknown or poorly quantified.

Dendroecological studies provide valuable information about historic influences of climatic variability on tree growth and forest productivity. At sites where growth is consistently limited by a small number of climate-related environmental stresses (hereafter, "limiting factors"), variations in tree-ring widths are correlated with climatic variables associated with those limiting factors (Fritts 1976). By identifying these climate-related limiting factors and the magnitudes of their influence through dendroecological analyses, we can better understand climatic influences on species geographic ranges and make more informed predictions about possible forest responses to future climatic scenarios.

We used dendroecological methods with a structured sampling approach to study regional growth responses to climatic variability in subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), a common subalpine tree species in the Pacific Northwest and throughout much of western North America (Franklin and Dyrness 1988; Alexander et al. 1990). We analyzed radial growth patterns from 28 tree-ring chronologies developed from forest stands in the subalpine zone of the Cascade and Olympic Mountains of western Washington and northwestern Oregon, U.S.A. This area represents much of the southern extent of subalpine fir in the maritime range of the species. Our objectives were to quantify coherent growth patterns in subalpine fir at different geographic scales, identify the climatic variables most closely associated with annual and multidecadal growth variability, and draw inferences about the limiting factors that control growth responses of this species to climatic variability in the Pacific Northwest.

We hypothesized that subalpine fir tree-ring chronologies from sites with similar climates should display similar annual and decadal growth patterns, regardless of geographic distance. Regional studies of tree growth responses to climatic variability have reported broad spatial coherence in growth patterns (Brubaker 1980; Cook and Cole 1991; Meko et al. 1993; Hofgaard et al. 1999; Peterson and Peterson 2001). Regional coherence in tree-ring growth patterns suggests that the climate-related factors limiting tree growth are similar within the region and that similar growth patterns are the result of common responses to regional climatic variability. If this is generally true, development and analysis of relatively few tree-ring chronologies may be sufficient to establish climate–growth relationships that can be applied throughout a climatically homogeneous region.

Within a species geographic range, however, environmental conditions vary along climatic and topographic gradients at different spatial scales, creating the potential for spatial heterogeneity in environmental limiting factors and associated tree growth responses to climatic variability. In the Olympic Mountains, Ettl and Peterson (1995*a*, 1995*b*) reported that climate–growth relationships in subalpine fir varied between wet and dry sites, apparently because site water balances were sufficiently different to produce different limiting factors. Variation in limiting factors and climate–growth relationships has also been observed across elevational gradients, presumably in response to variation in mean annual temperatures and site water balances (Kienast et al. 1987; Ettl and Peterson 1995*b*; Buckley et al. 1997). Therefore, we also hypothesized that subalpine fir growth patterns and climate–growth relationships would vary along annual precipitation and temperature (elevation) gradients, in response to variation in the dominant growth-limiting factors.

Study area

The study region has a maritime climate featuring cool, wet winters and warm, relatively dry summers. Annual precipitation varies considerably within the region, largely because of strong orographic effects (Franklin and Dyrness 1988). The Cascade and Olympic mountain ranges form barriers to the eastward movement of moist air masses from the Pacific Ocean, producing high precipitation on the western slopes and reduced precipitation on the eastern slopes. Mean annual precipitation ranges from over 500 cm in the southwestern Olympics and 300 cm in the western Cascades to less than 100 cm in the northeastern Olympics and eastern Cascades. At high elevations throughout the region, a large percentage of annual precipitation falls as winter snow, forming a deep snowpack that persists into the summer months.

Regional variations in mean annual precipitation, temperature, and snowpack produce different subalpine forest communities. On the wet, windward slopes of the Olympic and Cascade Mountains, subalpine fir occurs mostly within a narrow elevational band in the upper subalpine zone (Brooke et al. 1970; Franklin and Dyrness 1988) and as a pioneer species invading subalpine meadows and disturbed areas (Brink 1959; Franklin et al. 1971; Agee and Smith 1984; Woodward et al. 1995). As these forests mature, subalpine fir is gradually replaced by its more shade-tolerant associates, mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière), Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), and Alaska yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach).

On the drier, leeward slopes of these mountains, subalpine fir is commonly associated with Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), alpine larch (*Larix lyallii* Parl.), and whitebark pine (*Pinus albicaulis* Engelm.). Subalpine fir is more shade tolerant than these associates and can dominate older stands in these drier habitats. Low soil moisture limits seedling establishment and survival, however, especially on open south-facing slopes (Little et al. 1994).

Methods

Chronology development

We sampled subalpine forest stands at nine locations in the Cascade and Olympic Mountains of western Washington and northwestern Oregon where subalpine fir was a dominant or codominant species (Fig. 1). Sampling locations were chosen to represent the range of climatic conditions under which subalpine fir occurs in this area. At most locations, we selected three sites for tree-ring chronology devel-

opment that spanned the local elevational range of subalpine fir: one near the upper limit, one near the lower limit, and one near the middle (Table 1). The vertical distance between the upper and lower sites averaged 350 m and ranged from 170 m at Lake Minotaur to 460 m at Blue Mountain. Sites were mostly on south- to west-facing slopes, where subalpine fir is most typically found in the wetter portions of the Olympic Mountains and western Cascades (Fonda and Bliss 1969; Brooke et al. 1970; Franklin and Dyrness 1988). Six sites were chosen at Harts Pass in the eastern Cascades, four of which were on north-facing slopes (Peterson and Peterson 1994).

At each site, increment cores were collected from 9 to 30 dominant or codominant subalpine fir trees (Fig. 2). Trees were selected to be at least 80 years old with little or no visible damage to crowns or stems. Two increment cores were extracted from opposite cross-slope sides of each tree. Cores were stored in paper straws for transport, air-dried in the laboratory, and mounted on grooved boards. Mounted cores were sanded with progressively finer grades of sandpaper to produce a flat, polished surface on which tree-ring boundaries were clearly visible under magnification.

Tree-rings were dated using ring counts. Accuracy of assigned years was assured using standard cross-dating procedures (Stokes and Smiley 1968). One core per tree was selected for measurement based on the length and quality of the ring-width record. Rings were measured to the nearest 0.01 mm using a moving-stage measuring device (Robinson and Evans 1980) to produce a ring-width time series for each tree. Following measurement, cross-dating accuracy was rechecked using the program COFECHA (Holmes 1983).

Tree-ring growth chronologies ("site chronologies") were created for each site by removing low-frequency growth trends from each ring-width time series, converting ring widths to growth indices, and averaging growth indices by year for all sampled trees. This was done using the program ARSTAN (Cook and Holmes 1996). Low-frequency growth trends were removed by fitting a cubic spline curve with a 50% cutoff frequency of 100 years to each ring-width time series. Growth index time series were created for each tree by dividing the ring-width measurement for each year by the spline curve value for that year. Site chronologies were then created by averaging the component growth index time series by year, using a biweight robust mean (Cook et al. 1990).

Chronology growth pattern analysis

Three statistics were calculated to describe key properties of each site chronology. Mean sensitivity (MS) was used to describe year-to-year variation in ring widths as a proportion of mean ring width (Fritts 1976). The chronology MS statistic was the mean of MS values for the component ring-width series. A common variance statistic was calculated as the fraction of variance in the component growth index series captured (explained) by the first eigenvector in a principal components analysis. This common variance statistic provides an upper bound on the proportion of within-site growth variability that can be represented by the site chronology. The autocorrelation structure of each site chronology was described by the autoregressive error terms (at lags of 1–3 years) required to remove serial autocorrelation from the

Fig. 1. Locations at which subalpine fir tree-ring chronologies were developed. See Table 1 for full location names and site characteristics.
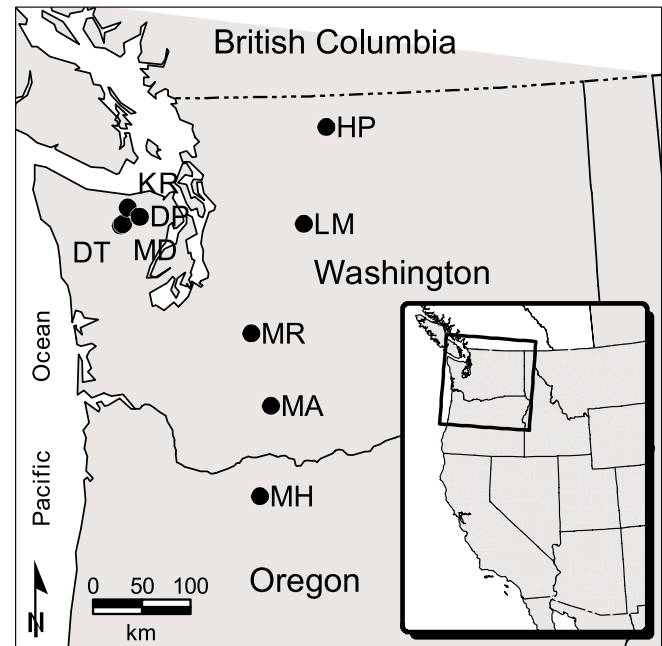
chronology time series and the proportion of variance explained by the corresponding autoregressive model.

Factor analysis (Johnson and Wichern 1992) was used to describe the correlation structure among the site chronologies and to extract a small number of "factor chronologies" that contained the common growth patterns from the 28 site chronologies. The number of factors included in the factor analysis was determined by running principal components analysis on the site chronologies and selecting the number of principal components for which the variance explained was at least 5%. Oblique (Promax) rotation of factors (SAS Institute Inc. 1999, PROC FACTOR) ensured that the resulting factor scores (factor chronologies) represented actual growth patterns rather than statistical extrapolations. Squared correlation coefficients (r^2) were used to describe associations between site chronologies and factor chronologies. Coefficients of multiple determination (R^2) were used to describe the total variance in each site chronology that could be explained when regressed against all the factor chronologies (communality statistic).

Climatic data

We obtained monthly divisional temperature and precipitation records (National Climate Data Center, Asheville, N.C.) for three climatic divisions in western Washington: the western Cascades (WA-5), the eastern Cascades (WA-6), and the Cascade–Olympic foothills (WA-4). Divisional climatic records were chosen over individual station records, because most sites had no nearby climate-recording stations with a sufficiently long period of record. Divisional climatic records also seemed more appropriate for studying climate–growth relationships associated with the growth patterns in the factor chronologies, because those growth patterns were associated with multiple sites. Site chronologies were

Table 1. Site descriptions for subalpine fir chronologies, including location, associated climatic division, mean annual precipitation for each sampling location.

Location name	Location code	Latitude (N)	Longitude (W)	Climate division	Precipitation (cm)	Site code	Elevation (m)	Aspect
Mount Hood	MH	45°20′	121°40′	WA-5	276[a]	M	1770	S
Mount Adams	MA	46°10′	121°30′	WA-5	253[a]	L	1465	SE
						M	1735	SW
						H	1890	W
Mount Rainier	MR	46°50′	121°45′	WA-5	296[a]	L	1540	S
						M	1645	W
						H	1840	S
Lake Minotaur	LM	47°50′	121°00′	WA-5	224[a]	L	1570	SE
						M	1630	S
						H	1740	S
Dodger Point	DT	47°50′	123°31′	WA-4	~350[b]	L	1395	SW
						M	1525	SW
						H	1725	SW
Mount Dana	MD	47°51′	123°29′	WA-4	~350[b]	L	1540	SW
						M	1675	SW
						H	1860	SW
Klahhane Ridge	KR	48°00′	123°25′	WA-4	~125[b]	L	1375	SW
						M	1560	SW
						H	1820	SW
Blue Mountain	DP	47°55′	123°15′	WA-4	~125[b]	L	1340	SW
						M	1595	SW
						H	1800	SW
Harts Pass	HP	48°43′	120°39′	WA-6	134[a]	L	1495	S
						H	1825	S
						V1	1875	NE
						N1	1925	NE
						V2	1825	NE
						N2	2000	NE

Note: Elevation and aspect are listed for each chronology site. Site codes indicate that chronologies were developed from stands near the upper elevation limit (H), the midrange elevation (M), and the lower elevation limit (L) for subalpine fir at that location.

[a]From nearby SNOTEL station, mean and standard deviation for 1989–1998.

[b]From Ettl and Peterson (1995b).

matched with the appropriate climate division prior to analysis (Table 1). Factor chronologies were assigned to climate divisions corresponding to the site chronologies with which they were most strongly correlated.

To investigate snowpack influences on growth, we obtained spring snowpack records from three locations distributed across the study region: Mount Rainier (Paradise, since 1921), Harts Pass (since 1941), and Hurricane Ridge (since 1950). These stations each have a long and complete snowpack monitoring record, and spring snowpack measurements at these sites are generally well correlated with those at nearby stations. However, no long-term records were available for the wetter areas in the central and southwestern Olympic Mountains, so we cannot be certain that annual snowpack anomalies at Hurricane Ridge are representative of that region. Snowpack variables of interest included spring snow depth and water content (April 1 or May 1), and the date of complete snowmelt (available at Mount Rainier only).

Previous studies have found significant correlations between tree growth patterns in western North America and indices of sea-level pressure anomalies and sea-surface temperatures in the Pacific Ocean (Biondi et al. 1997; Wiles et al. 1998; Peterson and Peterson 2001). The Pacific Decadal Oscillation (PDO), one such index, describes variations in spatial patterns of sea-surface temperatures in the North Pacific that are associated with variations in winter temperature, precipitation, and snowpack accumulations in the Pacific Northwest (Mantua et al. 1997; Zhang et al. 1997). Positive PDO values are associated with warmer, drier winters and reduced snowpack, while negative values are associated with cooler, wetter winters and increased snowpack. The PDO has received significant attention, because although index values vary at annual and shorter time scales, there is also significant persistence with apparent regime shifts at 20- to 30-year intervals. To assess the potential of the PDO as a surrogate for predicting short- and long-term growth anomalies in subalpine fir forests, we included a time series of mean winter PDO values (November to March) since 1921 as a climatic variable in the climate–growth analyses.

Climate–growth relationships

Correlation analysis was used to describe associations between growth variability and climatic variability for the period 1921–1990. Product–moment correlations (r) and

Fig. 2. Chronology descriptive statistics are displayed for all site chronologies, including the number of trees sampled for each chronology, mean sensitivity, common variance, the autoregressive (AR) model terms required to remove temporal autocorrelation, and the proportion of chronology variance explained by AR model. Vertical reference lines are mean values over all sites chronologies.
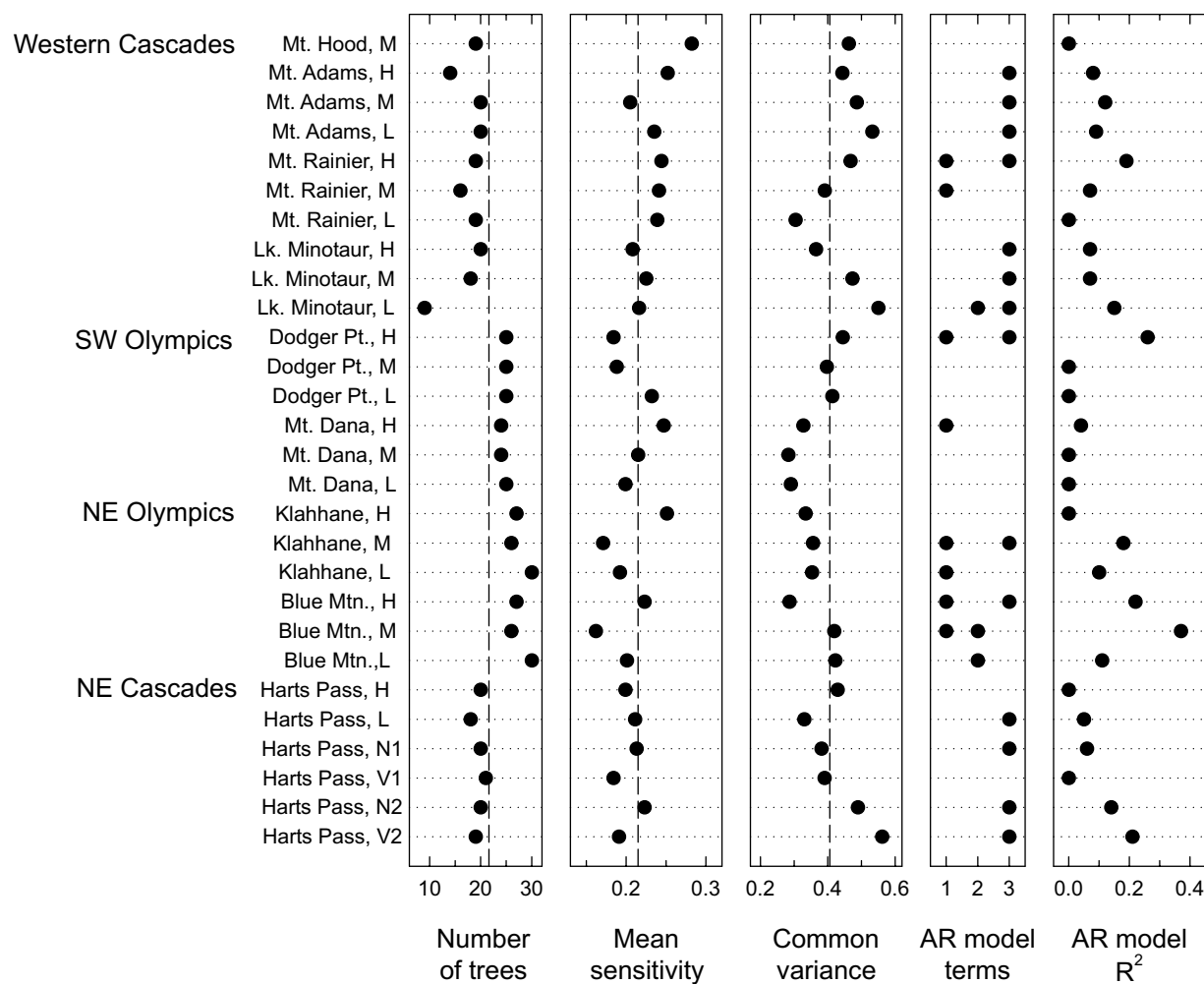
coefficients of determination from simple linear regression analyses (r^2) were calculated to describe associations between factor chronologies and monthly climatic variables for 24 months prior to the end of the growing season in which tree rings were formed (two hydrologic years, October–September). Seasonal climatic variables were created and included in the correlation analysis when two or more consecutive months showed strong positive or negative correlations between growth and climate (temperature or precipitation). Seasonal variables were formed by simple averaging of monthly climatic variables.

Results

Chronology growth patterns

Subalpine forests on high-precipitation sites in the western Cascades displayed the greatest annual variations in growth, with chronologies from Mount Rainier, Mount Hood, and Mount Adams having particularly high mean sensitivities (Fig. 2). Chronologies from drier sites in the NE Olympics and at Harts Pass displayed the smallest annual growth variations. There was no consistent pattern of variation in MS with respect to elevation within locations.

Common variance ranged from 0.28 to 0.54, indicating significant variation in the uniformity of tree growth patterns (and presumably tree growth responses to climatic variability) within sites (Fig. 2). Chronologies from two locations in the Olympic Mountains, Mount Dana, and Klahhane Ridge, had particularly low values (0.28–0.36), indicating considerable heterogeneity in annual and decadal growth patterns at those sites. Again, there were no consistent trends in common variance along elevation gradients.

Time-series analyses of the site chronologies showed considerable variation in autocorrelation structure. Half of the site growth chronologies (14 of 28) had significant autocorrelation at a lag of 3 years, three had significant autocorrelation at a lag of 2 years, and eight had significant autocorrelation at a lag of 1 year (Fig. 2). Nine chronologies had no significant autocorrelation. Autocorrelation accounted for 0–37% of the variance in the site chronologies (Fig. 2). Autocorrelation structure showed some consistency within sites and regions but was apparently insensitive to elevation.

Four common growth patterns were extracted from the 28 site chronologies using factor analysis. Four factors were used after principal components analysis showed that four

Table 2. Eigenvalues and variance explained from principal components and factor analyses of growth patterns from subalpine fir site chronologies for the period 1895–1990.

Eigenvector	Principal components analysis			Factor analysis	
	Eigenvalue	Variance (%)	Cumulative variance	Eigenvalue	Variance (%)
1	13.07	47.7	47.7	11.06	39.5
2	2.77	9.9	56.6	7.10	25.4
3	1.98	7.1	63.6	5.90	20.9
4	1.62	5.8	69.4	5.80	20.7
5	1.37	4.9	74.3		
6	1.14	4.1	78.4		

Fig. 3. Time-series plots of subalpine fir factor chronologies for the period 1895–1990.
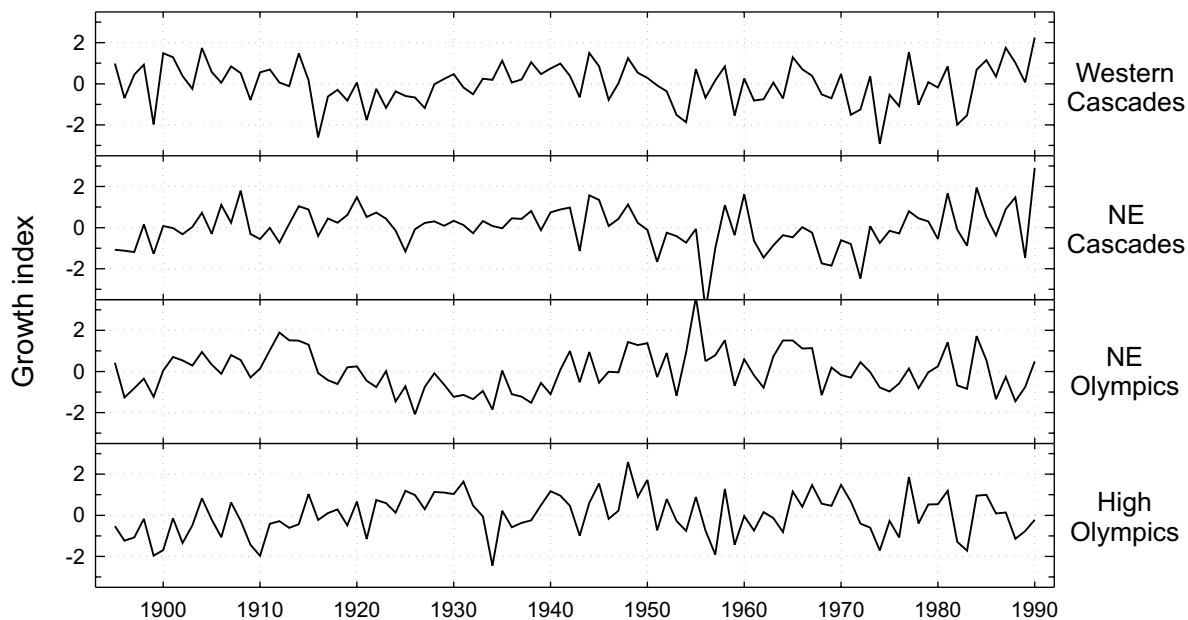
principal components (PCs) could account for 69% of the variance in the site chronologies and that additional PCs each explained less than 5% additional variance (Table 2). A single PC captured almost half of the variance (47%), indicating considerable similarity in growth patterns within the region. Oblique rotation produced four factors that each explained 21–40% of the total variance in the subalpine fir site chronologies.

The factor scores can be interpreted as time series of annual growth shared by multiple site chronologies (Fig. 3). These time series are hereafter called factor chronologies (FCs). Squared correlation coefficients (r^2) showed significant geographic patterns in associations between site chronologies and factor chronologies (Fig. 4, Table 3). The first FC contained a growth pattern shared by chronologies from the western Cascades and SW Olympics; it was named the western Cascades FC. The second FC contained a growth pattern shared by chronologies from high- and middle-elevation sites at Harts Pass; it was named the NE Cascades FC. The third FC contained a growth pattern shared by chronologies from low- and middle-elevation sites in the NE Olympics, the high-elevation site at Dodger Point, and the low-elevation site at Harts Pass; it was named the NE Olympics FC. The fourth FC contained a growth pattern shared by three high-elevation sites in the Olympic Mountains; it was

named the high Olympics FC. In most cases, site chronologies were highly correlated with only one or two FCs.

Coefficients of multiple determination (R^2) showed that together the four factor chronologies captured 47–81% of the variance in the site chronologies (Table 4). These values were less than the sum of the individual coefficients of determination (r^2), because the factor chronologies were positively correlated with one another, with correlation coefficients ranging from 0.16 to 0.48. The positive correlations were the result of positive correlations among the site chronologies that were preserved by the oblique rotation method in the factor analysis.

Time-series analysis of the FCs showed that all FCs except the high Olympics had significant autocorrelation at a lag of 3 years. The NE Olympics FC also had significant autocorrelation at a lag of 1 year. Autocorrelation accounted for 6–8% of the variance in the Western Cascades and NE Cascades FCs and 20% of the variance in the NE Olympics FC. There was no significant autocorrelation in high Olympics FC.

Climate–growth relationships

Climatic variables associated with winter snowpack were the best predictors of annual growth variations for three of the four factor chronologies. The western Cascades and NE

Fig. 4. Time-series plots of selected subalpine fir site chronologies for the period 1850–1990. Chronologies are grouped based on correlations with factor chronologies (see Table 3).
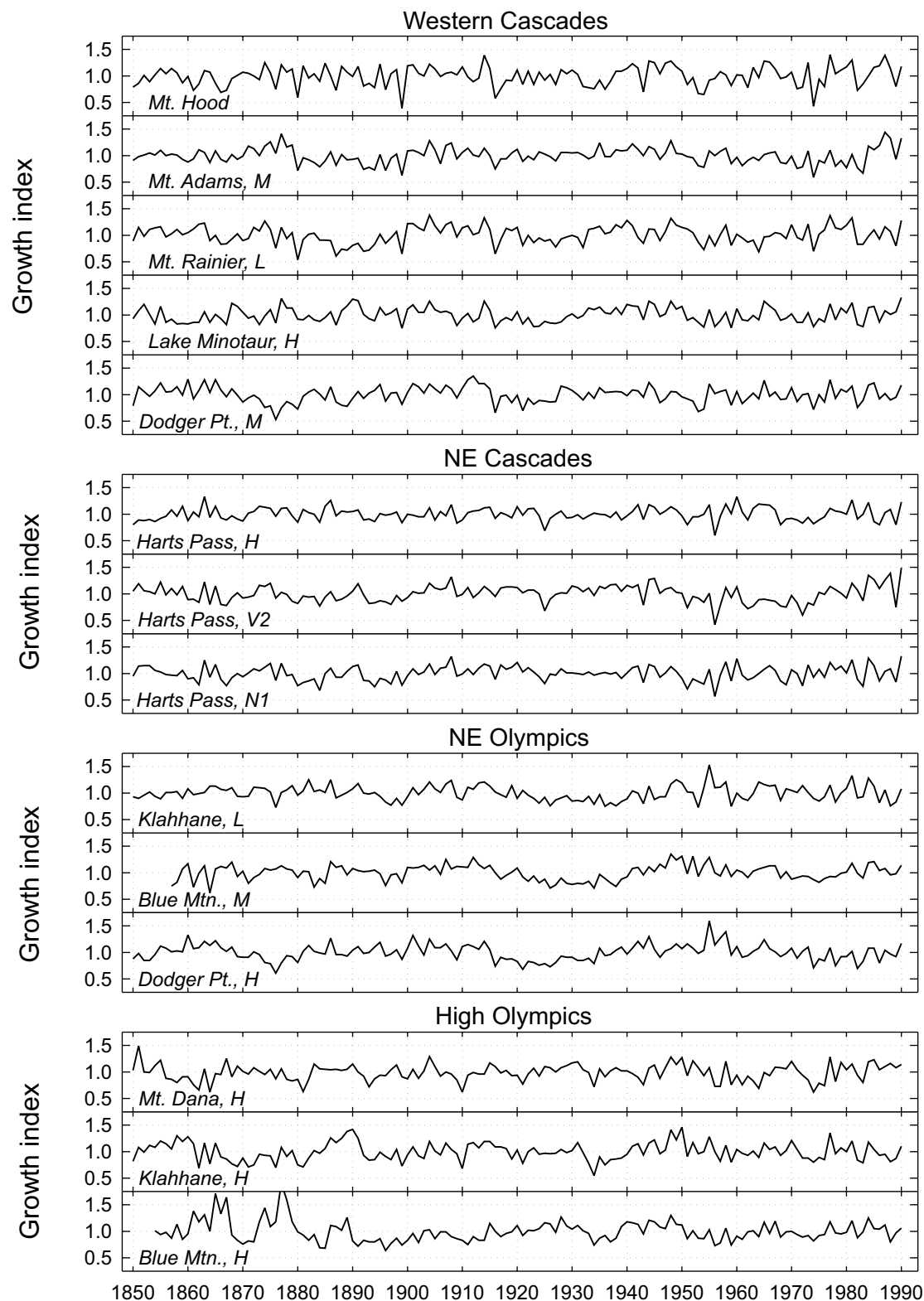
Cascades FCs were negatively correlated with spring snowpack depth and snowpack water content at Mount Rainier, Harts Pass, and Hurricane Ridge (Table 5). Winter precipitation, the source of snow, was negatively correlated with growth for the Western Cascades, NE Cascades, and

high Olympics FCs, accounting for 20–27% of the growth variance (Table 5). All three FCs were also negatively correlated with annual precipitation (Table 5), of which winter precipitation is a large fraction. The western Cascades and NE Cascades FCs were also positively correlated with

Table 3. Squared product–moment correlations (r^2) between site chronologies and factor chronologies.

		Site										
	Elevation	MH	MA	MR	LM	DT	MD	KR	DP	HP1	HP2	HP3
Western Cascades FC	Upper		0.28*	0.55*	0.75*	0.43	0.21	0.16	0.10	0.20	0.31	0.29
	Middle	0.64*	0.72*	0.46*	0.74*	0.65*	0.53*	0.32	0.13		0.15	0.27
	Lower		0.59*	0.61*	0.68*	0.45*	0.54*	0.11	0.00	0.19		
NE Cascades FC	Upper		0.03	0.22	0.30	0.01	0.13	0.10	0.19	0.55*	0.76*	0.77*
	Middle	0.19	0.28	0.32	0.31	0.09	0.07	0.18	0.05		0.53*	0.83*
	Lower		0.14	0.26	0.28	0.15	0.08	0.04	0.01	0.21		
NE Olympics FC	Upper		0.19	0.01	0.15	0.52*	0.03	0.39	0.05	0.24	0.13	0.01
	Middle	0.12	0.08	0.01	0.03	0.28	0.24	0.45*	0.70*		0.08	0.01
	Lower		0.04	0.07	0.08	0.12	0.21	0.79*	0.48*	0.33*		
High Olympics FC	Upper		0.28	0.24	0.18	0.03	0.59*	0.59*	0.65*	0.08	0.16	0.17
	Middle	0.21	0.15	0.30	0.19	0.11	0.32	0.06	0.05		0.18	0.09
	Lower		0.01	0.12	0.04	0.44	0.29	0.12	0.17	0.01		

*Factor chronology most highly correlated with each site chronology.

Table 4. Communality statistics describe the total variance in each site chronology that is explained by multiple regression on the four factor chronologies.

	Site										
Elevation	MH	MA	MR	LM	DT	MD	KR	DP	HP1	HP2	HP3
Upper		0.47	0.65	0.79	0.77	0.63	0.78	0.69	0.69	0.83	0.81
Middle	0.68	0.74	0.64	0.80	0.73	0.69	0.61	0.71		0.59	0.85
Lower		0.63	0.64	0.73	0.65	0.67	0.80	0.63	0.53		

spring temperature in the growth year, a climatic variable that influences the form of spring precipitation (rain or snow) and the start of spring snowpack consolidation and snowmelt.

Summer temperature and precipitation were good predictors of growth variability for all the factor chronologies, but the growth responses to these factors varied (Table 5, Fig. 5). For the snow-dominated FCs, growth was either positively correlated with summer temperature in the growth year (NE Cascades and high Olympics) or negatively correlated with summer precipitation in the growth year (western Cascades). Growth was negatively correlated with previous summer mean temperature (July–August) for western Cascades and high Olympic FCs (Table 5, Fig. 5), accounting for 8–9% of the growth variance.

Previous summer temperature and precipitation were much stronger predictors of growth for the NE Olympics FC. Previous summer temperature was negatively correlated with growth in the NE Olympics FC, accounting for 25% of the variance. Growth in the NE Olympics FC was also positively correlated with previous summer precipitation and negatively correlated with spring temperature in the growth year.

Autumn mean temperature (October–November) was positively correlated with subalpine fir growth in the western Cascades and NE Cascades FCs (Table 5). The NE Olympics growth pattern was positively correlated with November temperature but not the broader autumn temperature variable. The high Olympics growth pattern showed no sensitivity to autumn temperature.

Climate–growth relationships for individual site chronologies were generally similar to those for the factor chronologies with which they were closely associated, but the variance explained by the major climatic variables varied substantially (Fig. 6). For example, among-site chronologies most closely associated with the western Cascades FC, the growth variance explained by winter precipitation varied from 8% at the low-elevation site on Mount Rainier to 37% at the Mount Hood site. Similarly, among the site chronologies most closely associated with the NE Olympics FC, the growth variance explained by previous summer temperature varied from 10% to almost 33%.

Relationships between growth and winter PDO varied by region; the time scales at which responses were observed also varied considerably. Scatterplots and correlation statistics showed that subalpine fir growth in the NE Cascades was positively correlated with annual variations in the winter PDO (Fig. 7). Furthermore, the PDO and NE Cascades FC showed similar low-frequency trends through time, when both series were smoothed with a 5-year running mean (Fig. 7). The western Cascades FC showed a similar, but weaker, relationship. In contrast, the NE Olympics FC was negatively correlated with winter PDO at a lag of 1 year (Table 5), and smoothing showed low-frequency variation in growth that mirrored variations in the PDO (Fig. 7). The high Olympics FC showed no relationship between growth and winter PDO.

Multiple-regression models with autoregressive error terms were created for all four FCs to describe the joint effects of climatic variability on subalpine fir growth (Table 6). The final models accounted for 49–58% of growth variance in the factor chronologies. Models for all but the NE Cascades FC required first-order autoregressive error terms to account for positive serial autocorrelation in model

Table 5. Relationships between temporal variability in factor chronologies and seasonal climatic variables.

Climate variable	Western Cascades	NE Cascades	NE Olympics	High Olympics
Spring temperature, previous year (Mar.–Apr.)	0.06	0.15	—	—
Summer temperature, previous year (July–Aug.)	–0.09	—	–0.25	–0.08
Summer precipitation, previous year (July–Aug.)	—	—	0.13	—
Autumn temperature, growth year (Oct.–Nov.)	0.08	0.13	—	—
Winter precipitation, growth year (Dec.–Mar.)	–0.27	–0.20	—	–0.21
Spring temperature, growth year (Mar.–Apr.)	—	0.06	–0.17	—
Summer temperature, growth year (July–Aug.)	—	0.08	—	0.09
Summer precipitation, growth year (July–Aug.)	–0.07	—	—	—
Annual temperature, growth year	0.08	0.11	–0.08	
Annual precipitation, growth year	–0.20	–0.19	—	–0.16
Snow depth, Mount Rainier, May 15	–0.22	–0.10	0.07	—
Snow water content, Hurricane Ridge, April 1	–0.19	–0.20	—	—
Snow water content, Harts Pass, May 1	–0.44	–0.29	—	–0.10
Summer southern oscillation index, previous year	—	–0.14	—	—
Pacific Decadal Oscillation index, growth year	0.13	0.35	–0.08	—
Pacific Decadal Oscillation index, previous year	—	0.07	–0.14	—

Note: Values are squared correlation coefficients with sign retained to indicate the nature of the relationship ($r^2 \times \text{sign}(r)$). All values shown are statistically significant ($p < 0.05$).

residuals. Predictor variables included in the final models were generally consistent with those reported from the correlation analysis, the most notable exception being the NE Cascades FC, for which the model included previous summer temperature and excluded growth year summer temperature (opposite of correlation analysis).

Discussion

Chronology growth patterns

Subalpine fir tree-ring chronologies developed from climatically similar sites have similar patterns of annual growth variations over the past century, consistent with our first hypothesis. Similar growth patterns suggest that the same climatic factors limit growth at many sites and that the magnitude of growth limitation is influenced synchronously by regional climatic variability. This regional climatic variability influences tree growth at both annual and decadal time scales in some areas. Differences in tree growth patterns between sites can be the result of local variation in the climatic factors that influence a direct limiting factor (e.g., the relative influence of winter temperature and precipitation on snowpack accumulation) (Villalba et al. 1994) or trends in climate-related limiting factors across climatic gradients (Ettl and Peterson 1995b).

We found four common temporal patterns of growth variability shared by chronologies developed at geographically distant sites. The sites associated with each pattern appear to share similar characteristics with regard to annual precipitation and annual water balance. However, assumed differences in mean annual temperatures between upper and lower sites at each location had no consistent effect on chronology growth patterns.

Site chronologies associated with the western Cascades FC all were developed from trees growing on wet, cold sites with high amounts of annual precipitation and deep snowpacks that persist well into the summer (Brink 1959;

Brooke et al. 1970; Evans and Fonda 1990). Soils remain near freezing temperatures until snowmelt is complete, after which they warm rapidly and track mean daily temperatures (Evans and Fonda 1990; Woodward 1998). Snowmelt dates vary by up to 6 weeks in response to annual variability in climate (Peterson and Peterson 2001). Mountain hemlock and Pacific silver fir are common associates on these sites, so subalpine fir is a seral species except on the driest microsites. Ettl and Peterson (1995b) reported growth similarities among chronologies from middle- and low-elevation sites in the SW Olympics; our analysis shows that this growth pattern is widespread, being shared by subalpine fir stands in the western Cascades as well.

Chronologies associated with the NE Olympics FC were developed from warmer, drier sites with lower annual precipitation and earlier snowmelt. Douglas-fir is a common associate on these sites. Although this pattern was observed primarily in the NE Olympics, the chronology from the low-elevation site at Harts Pass had a similar growth pattern, suggesting that the response may be typical of low-elevation, dry sites. Additional subalpine fir chronologies from stands in the eastern Cascades and interior Columbia River basin would be needed to resolve this issue.

Chronologies associated with the NE Cascades FC were collected from neighboring stands at Harts Pass (Peterson and Peterson 1994), a relatively dry site in the eastern Cascades rain shadow. Harts Pass receives less precipitation annually than sites in the western Cascades but is also colder in the winter, so a large fraction of winter precipitation falls as snow. In an average year, snowmelt at Harts Pass occurs earlier than at sites in the western Cascades but later than at low-elevation sites in the NE Olympics.

The grouping of the high-elevation chronology from Mount Dana (a wet site) with the high-elevation chronologies from Klahhane Ridge and Blue Mountain (dry sites) is less easily interpreted. Ettl and Peterson (1995b) grouped these chronologies with other wet-site chronologies from

Fig. 5. Correlations (*r*) between subalpine fir factor chronologies and monthly climate variables for the period 1921–1990. Climate variables include total monthly precipitation (left column) and mean monthly temperatures (right column) for 24 months (two hydrologic years, October–September) prior to the end of ring formation. Bars indicate correlation coefficients, with threshold values for statistical significance at *r* = 0.24 (*P* < 0.05) and *r* = 0.30 (*P* < 0.01). Shaded areas indicate summer growth periods (June–August).
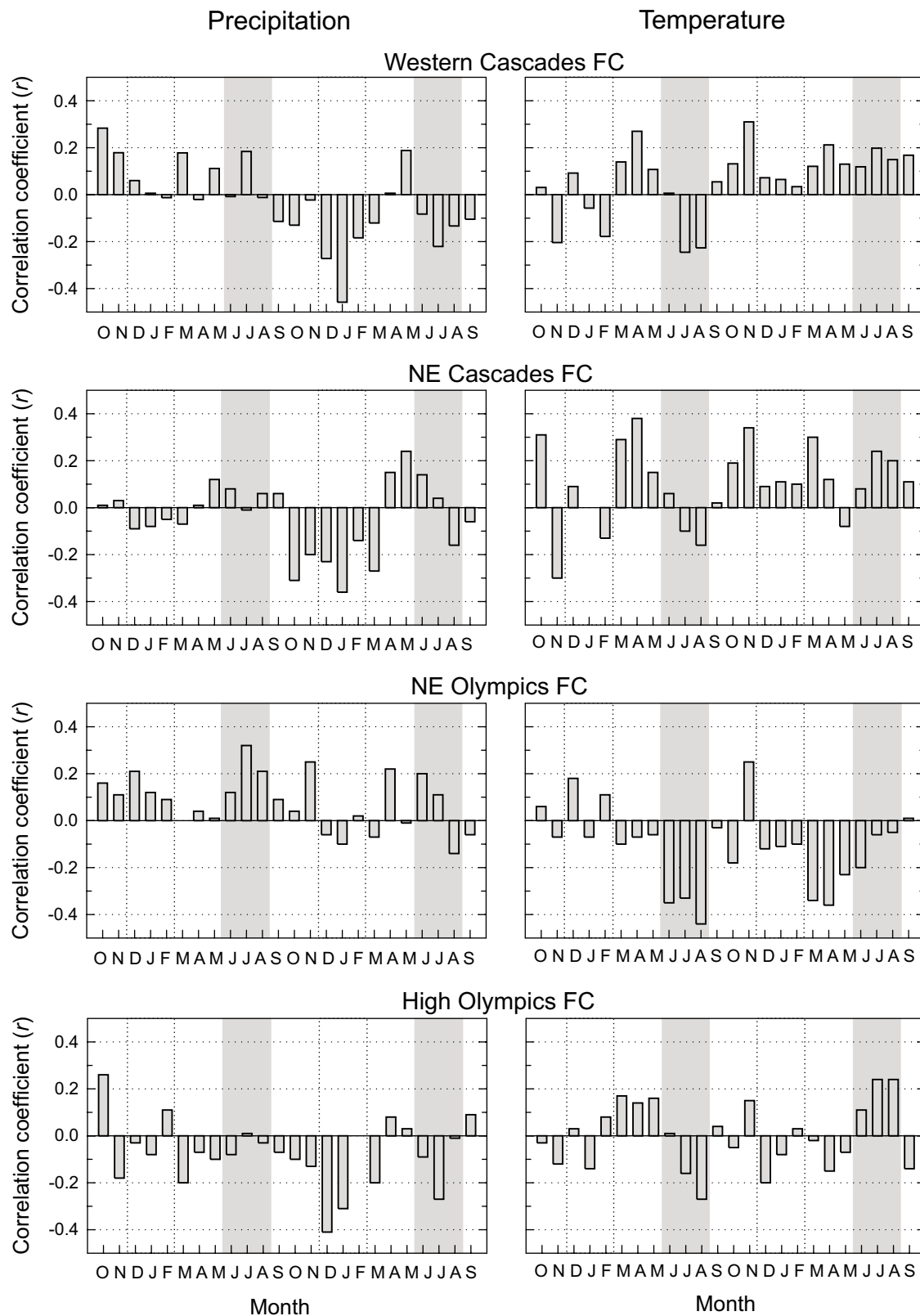
Fig. 6. Squared correlation coefficients (with sign retained) describe relationships between site chronology growth variations and annual variability in winter precipitation, spring snowpack water content, previous-year summer temperature, and growth-year summer temperature. Symbols indicate that site chronologies are most closely associated with the western Cascades (solid circles), NE Cascades (open circles), high Olympics (solid triangles), or NE Olympics (open triangles) factor chronology (see Table 3).
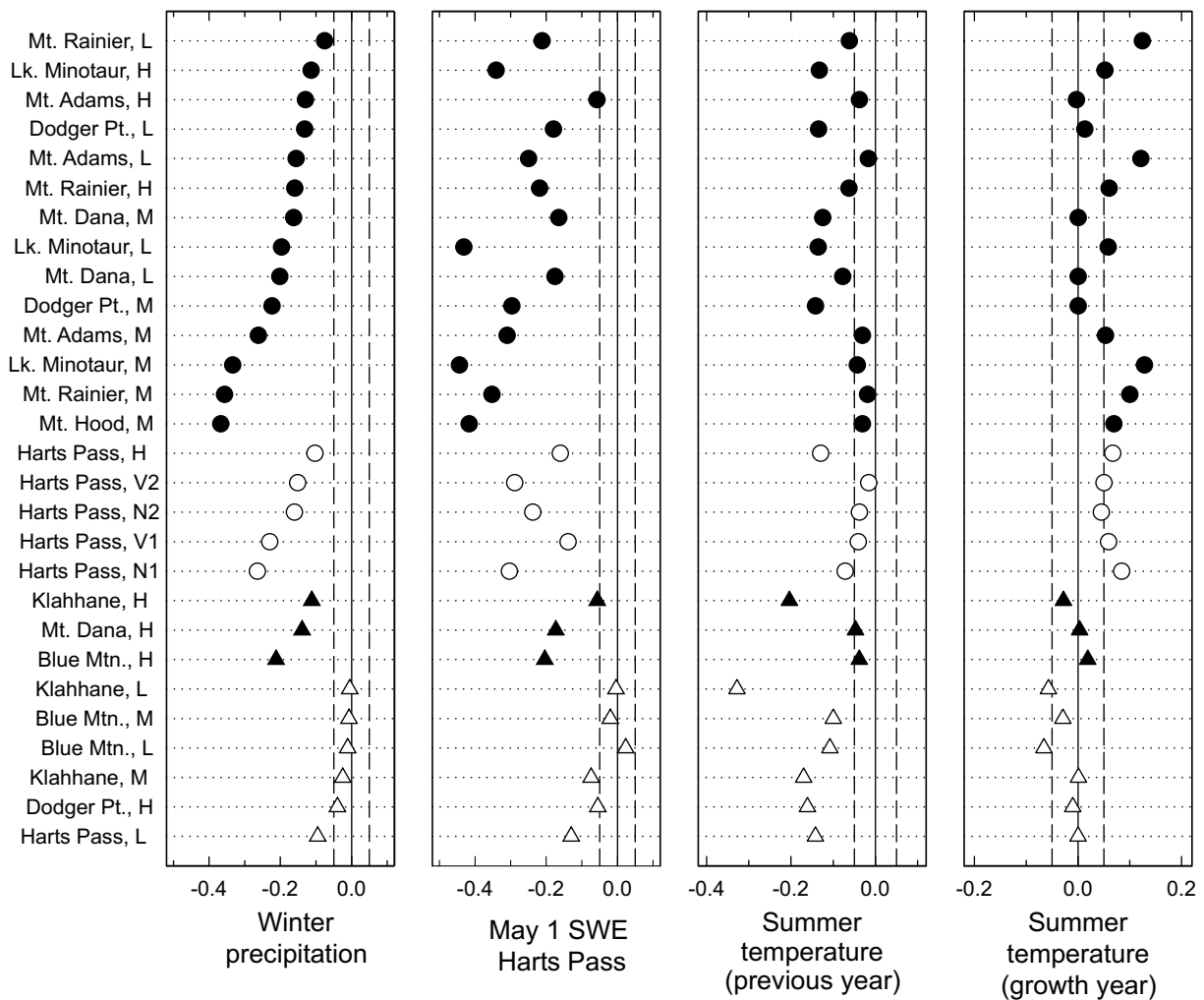
Mount Dana and Dodger Point. However, our factor analysis indicated that chronologies from this high-elevation group were poorly correlated with chronologies from the Cascades, from which the western Cascades growth pattern is largely derived.

Climate–growth relationships

Our analysis of climate–growth relationships suggests that differences in growth patterns among the four factor chronologies (and their associated site chronologies) are largely due to geographic variations in climatic means, biophysical environments, and associated environmental limiting factors, as predicted by our second hypothesis. Similar variations in tree growth responses to climate across regional climatic gradients have been reported in the Pacific Northwest and elsewhere for individual species (Keen 1937; Cook and Cole 1991; Mäkinen et al. 2000; Peterson and Peterson 2001) and for species mixtures (Brubaker 1980; Meko et al. 1993; Peterson and Peterson 1994).

Two of the four growth patterns (western Cascades and NE Olympics FCs) represented sites at opposite extremes of

a moisture-temperature gradient. The western Cascades FC represents sites in the wettest part of the range of subalpine fir in the Pacific Northwest, while the NE Olympics FC represents the driest sites from which subalpine firs were sampled. Climate–growth relationships were quite different for these two factor chronologies, indicating that the growth patterns were the result of different growth-limiting factors, not different patterns of annual climatic variability.

Annual growth of subalpine fir on the wet western slopes of the Cascades and Olympics appears to be limited primarily by late-melting snow and growing season length. Snowpack duration and growing season length also influences seedling establishment on these sites, with seedling cohorts establishing during periods with reduced snowpack (Brink 1959; Franklin et al. 1971; Woodward et al. 1995; Rochefort and Peterson 1996). Subalpine fir growth initiation in spring is linked to snowmelt and subsequent increases in soil temperature (Worrall 1983), so late snowmelt delays the start of the growing season. Because cessation of growth in high-elevation and high-latitude environments is at least partially controlled by photoperiod (Vaartaja 1959;

Fig. 7. Growth variations from subalpine fir factor chronologies are compared with high- and low-frequency variations in the winter PDO (November and March). Scatterplots show relationships between growth and the winter PDO in the growth year. Line graphs show 5-year running means of growth (black lines) and winter PDO (gray lines).
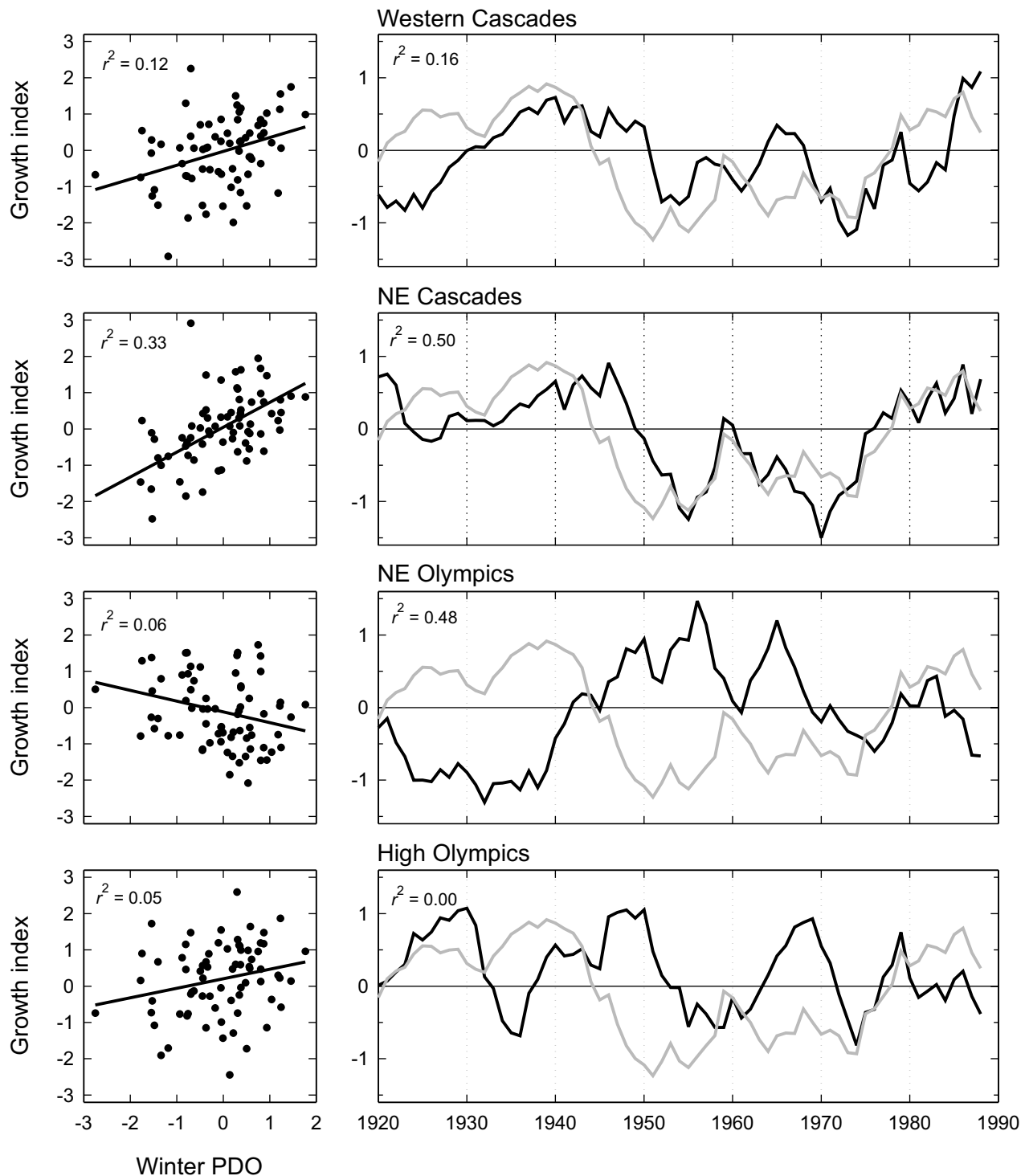
Oleksyn et al. 1998; Partanen and Beuker 1999), snowmelt dates influence both timing and duration of the period during which growth occurs. Strong correlations between snowpack duration (growing season length) and tree growth have also been reported for mountain hemlock forests (Heikkinen 1985; Graumlich and Brubaker 1986; Gedalof and Smith 2001; Peterson and Peterson 2001), suggesting a

general snowpack limitation on growth and productivity on the western slopes of the Cascades and Olympics (Peterson 1998).

On sites where growth is limited by late snowmelt, warm summer temperatures may positively influence growth by improving the length and quality of the growing season. Warm summer temperatures melt residual snow (extending

Table 6. Results from autoregressive modeling of factor chronology growth responses to climatic variability (1921–1990).

	Western Cascades	NE Cascades	NE Olympics	High Olympics
Model variable				
Summer temperature, growth year	+			+
June precipitation, growth year			+	
Spring temperature, growth year			–	–
Winter precipitation, growth year	–	–		–
Winter PDO index, growth year		+		
Autumn temperature, growth year	+	+		
Summer temperature, previous year	–	–	–	–
Summer precipitation, previous year			+	
Spring precipitation, previous year				–
Model statistics				
Autocorrelation coefficient (lag 1)	0.38	0.00	0.33	0.39
Model R^2	0.56	0.49	0.50	0.58

Note: Symbols indicate the (statistically significant) variables included in the final models and the signs of the coefficients. Model summary statistics include the first-order autocorrelation coefficient for the error term prior to inclusion of the autoregressive term and the total variance explained by the final model.

the growing season), raise soil and leaf temperatures (Evans and Fonda 1990), promote rapid root and shoot growth (Tranquillini 1979; Körner 1998), and reduce the frequency of low-temperature photoinhibition (Germino and Smith 1999). Warm (and dry) summer conditions may also indicate increased solar radiation, which can also limit forest growth and productivity on cloudy, wet sites. Because soil water is recharged by late-melting snow, summer soil moisture deficits are infrequent on these sites.

On the drier sites associated with the NE Olympics growth pattern, annual growth appears to be limited by soil water availability in the summer. Growth on these sites is negatively correlated with spring temperatures and positively correlated with early summer precipitation, suggesting that factors that delay snowmelt and reduce the severity and duration of summer soil water deficits are favorable for growth. Warm, dry summer conditions reduce growth the following year, probably by reducing net photosynthesis and the amount of stored carbohydrates available for early shoot and stem growth (Fritts 1976; Fritts and Swetnam 1989). These climate–growth relationships are similar to those reported for subalpine fir in the more continental climate of the Rocky Mountains; there, spring and summer temperature and, in some cases, summer precipitation are the primary factors associated with annual growth variability (Colenutt and Luckman 1991; Villalba et al. 1994).

The NE Cascades and high Olympics growth patterns appear to represent growth responses to climatic variability under cold, dry conditions. Despite receiving the same amount of annual precipitation as sites associated with the NE Olympics growth pattern, colder temperatures at these high-elevation sites produce climate–growth relationships that are closer to the western Cascades growth pattern than to the NE Olympics growth pattern. Like the western Cascades growth pattern, the NE Cascades and high Olympics patterns are sensitive to winter precipitation and, at least for the NE Cascades growth pattern, spring snowpack. Colder winter and spring temperatures at these high-elevation sites increase the

fraction of precipitation that falls as snow and retard snowmelt, delaying the start of the growing season but increasing water availability during the summer months. Spring snowpack may persist long enough at high elevations to produce a growing-season length limitation on growth, especially on north aspects, where most of the Harts Pass sites were established. Cooler summer temperatures probably also reduce summer drought stress by reducing evapotranspiration rates.

The different growth responses to variations in the PDO index also illustrate the importance of mean temperature and precipitation conditions. In the eastern Cascades (Washington climate division 6), negative values of the PDO index are associated with increased winter precipitation and cooler spring temperatures. This combination produces significantly higher snowpack because most of the extra winter precipitation falls as snow, and cooler spring temperatures slow the onset of rapid snowmelt. Spring (April 1) snow water content at Harts Pass shows a strong linear correlation with winter PDO ($r = -0.73$, $p < 0.001$). We, therefore, conclude that subalpine fir growth is correlated with PDO primarily because of the common association with spring snow depth and growing season length.

In the western Cascades, the PDO is correlated with both winter temperature ($r = 0.49$) and winter precipitation ($r = -0.46$). When the PDO is negative, winter precipitation increases and colder winter temperatures cause a higher proportion of winter precipitation to fall as snow, thereby increasing snowpack accumulations and delaying snowmelt. At high elevations, we would expect this additional snow to reduce growth, while lower, drier sites could benefit from the additional storage of water in the snowpack.

Conclusions

On the wet sites of the western Cascades and Olympics, late snowmelt and short growing seasons limit both the establishment and growth of subalpine fir trees throughout most of the species' elevation range. The lower limit of its

range on these sites is almost certainly the result of competition from species with greater shade tolerance but lower tolerance for deep snow and short growing seasons. On drier sites in the rain shadows of the Cascade and Olympic Mountains, subalpine fir trees experience drought stress near the lower limit of the species range. Although this drought stress is apparently not severe enough to kill mature trees, it may limit seedling establishment and survival.

General circulation models currently indicate that global mean temperatures may rise by 1–3°C over the next century in response to increasing atmospheric concentrations of greenhouse gases (Watson et al. 1996). Higher temperatures could significantly reduce snowpack accumulations in the Pacific Northwest by causing more winter precipitation to fall as rain (Mote 1999) and melting the remaining snowpack earlier. Any climatic-change scenario that significantly reduces snowpack duration is likely to increase the growth and productivity of established subalpine fir forests on wet sites in the Pacific Northwest by increasing mean growing season lengths. This response has been observed over the past century during extended periods when the PDO was in a warm phase (Fig. 5). However, on warm dry sites, where subalpine fir currently grows with Douglas-fir, warmer temperatures are likely to increase summer drought stress in mature trees and reduce seedling establishment and survival.

This study showed that regional networks of tree-ring chronologies can be used to better understand tree species growth responses to climatic variability and to identify the environmental factors limiting tree growth and forest productivity. If tree-ring chronology networks span the range of climatic and topographic conditions under which the target species occur, these regional dendroecological studies can be used to test assumptions about environmental constraints on species distributions. A common problem in these studies, however, is that site climate and biophysical information is often unavailable and must be estimated or inferred. If these data could be collected on site, or estimated accurately using geographic information system (GIS) based models, it would improve our ability to interpret the causes of site variations in chronology growth patterns and climate–growth relationships.

Acknowledgements

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